

Seeing the content of the mind: Enhanced awareness through working memory in patients with visual extinction

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In the present study, we demonstrate that parietal patients with visual extinction show enhanced awareness when there is a match between the current contents of their working memory and the stimuli presented in the visual field. This effect cannot be attributed to automatic bottom-up priming from the presentation of a memory cue, because extinction was reduced only when patients committed the cue to memory, and not when primes were viewed passively or merely identified. The results suggest that reentrant processes, from working memory, modulate awareness.

top-down processing | parietal damage | attention

Patients with visual extinction typically show reduced awareness for visual stimuli presented on the side of space contralateral to their brain lesion, when competing stimuli are presented on the ipsilesional, opposite side (1, 2). Despite this lack of awareness, there is evidence that contralesional stimuli are processed to some degree, so that extinction is reduced if these stimuli group with items falling on the ipsilesional side (2–5). Here we investigate whether top-down feedback from visual information held in working memory can enhance visual awareness in these patients. According to the biased competition model of visual selection (6), working memory plays a crucial role in resolving the competition between different objects for access to higher-level processing. At a neural level, the preactivation of objects in working memory can feed back to modulate neuronal responses in early visual cortex, when a target that matches the memory representation has to be selected for a response (7, 8). At a behavioral level, working memory affects the deployment of attention in visual space, biasing attention toward those objects that match the contents of memory (9) during early stages of visual processing and in an involuntary fashion (10, 11).

Results

The current study examined top-down effects from working memory in five patients with visual extinction due to lesions to the inferior parietal lobe (three with right unilateral, one with left unilateral, and one with bilateral lesions but showing left-side extinction; see Fig. 1) (12). Patients were asked to hold in memory a cue that was displayed for 1 sec at fixation at the beginning of each trial. After a 200-ms interval, either one or two target objects were displayed in the left or right visual field, with exposure duration for this display varying between 80 and 2,000 ms, depending on the patient (see *Methods* for details). The task was to report the color and shape of the target object(s). Memory cues and targets were simple geometric shapes (square, circle, triangle, or diamond) presented in one of three colors (red, blue, or yellow). On 57.14% of the trials, one object matched the memory cue; on the remaining trials, the memory cue and the target(s) differed. A memory probe was included on 20% of the trials, to make sure patients were maintaining the cue in memory. Performance on memory probe trials was good (mean 90% correct).

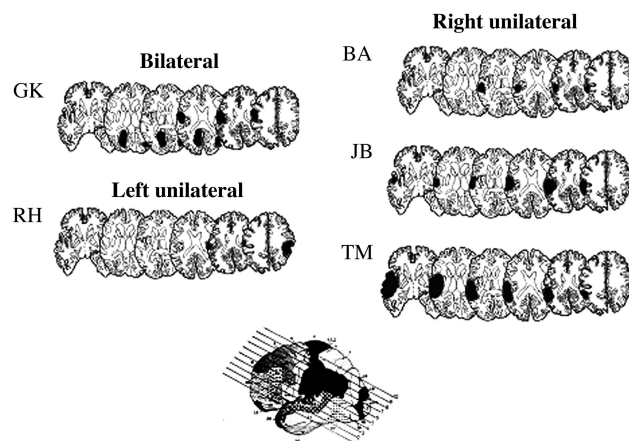


Fig. 1. Lesion reconstructions in the patients from MRI scans. Lesions have been redrawn onto standard slices. (Lower Left) The 10 slices used. Only slices three to eight are represented here. The left half of each slice represents the right hemisphere. For RH, the contralesional stimulus fell in the right visual field (12). All patients sustained damage to the inferior parietal lobe. GK, a 65-year-old right-handed businessman, had bilateral lesions affecting the right medial occipital parietal region (including the cuneus and precuneus), the right temporoparietal region, and the left temporoparietal region. RH, a 72-year-old left-handed plumber, had a lesion affecting the left inferior parietal and superior temporal lobes, including the angular gyrus. BA was a 50-year-old former manual worker with a lesion affecting his right parietal lobe (angular gyrus, supramarginal gyrus). JB was a 70-year-old left-handed housewife whose lesion affected the inferior parietal and frontal areas of her right hemisphere, including the angular and supramarginal gyri, the postcentral gyrus, and the inferior frontal gyrus. TM, a 69-year-old former publican, had damage to the right temporal and posterior parietal lobes, including the angular gyrus. All patients had suffered a stroke at least 4 years previously and were in a stable condition. All showed extinction under bilateral presentation conditions.

The correct reports of targets (hits) are shown in Fig. 24. False positives (reporting the memory item when it was absent) were minimal, mean 0.81%, and were corrected by subtracting these responses from the “hits” recorded when memory items were reported correctly. This result rules out a simple response bias account of performance, where patients guessed the memory stimulus when they failed to detect the target. A 2 (target visual field) \times 2 (matching) \times 2 (number of objects) ANOVA was conducted on the proportion of correct identifications. We found that, when the memory cue did not match a target, there was clear extinction; there was poor report of the contralesional stimulus, especially on two-object trials (when an ipsilesional

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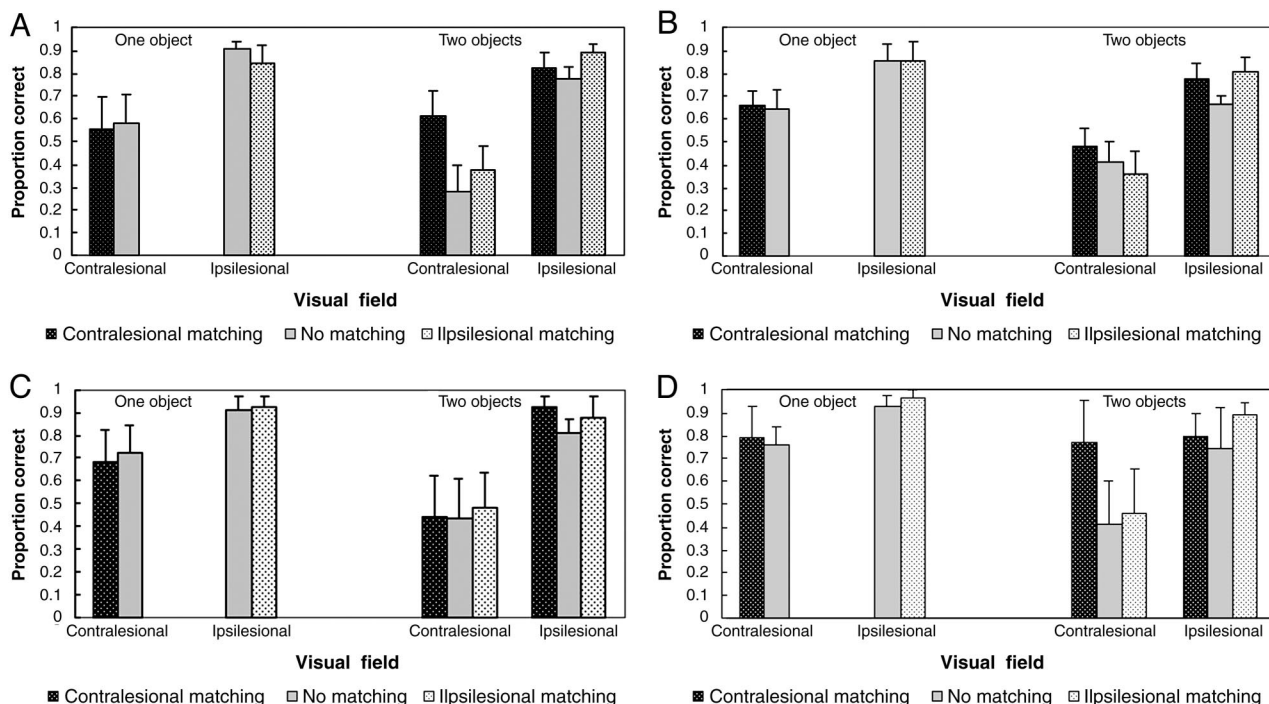


Fig. 2. Proportion of correct identifications of target(s) at each visual field, as a function of the matching between the prime and target stimuli (bars represent SEM). (A) Experiment 1, prime in working memory; (B) Experiment 2, priming only; (C) Experiment 3, prime processed to the level of identification; (D) Experiment 4, replication of Experiment 1 with primes displayed for 3 sec.

stimulus was presented simultaneously). However, there was a reduction in extinction in two-object trials for contralateral targets that matched the memory cue. These conclusions were confirmed by an interaction between whether targets matched the memory item (match vs. no match) and the visual field where the target was displayed [$F(1, 4) = 26.42, P = 0.007$, computed with Greenhouse–Geisser correction]. The number of items had a reduced effect when the memory cue matched a target, and this pattern was most striking for targets on the contralateral side. The effects of memory matching were absent on one-object trials [$F(1, 4) = 0.76$, ns]. To examine this pattern further, we assessed performance for contra- and ipsilateral targets as a function of the position of the memory item (contra- vs. ipsilateral vs. no matching). A 2 (target visual field) \times 2 (memory item field) ANOVA yielded a significant interaction between these two factors [$F(2, 8) = 14.74, P = 0.007$]. Contralateral targets were reported better when the memory cue reappeared in the contralateral relative to the ipsilateral field ($t = 5.76, P = 0.004$, two tailed), and relative to when the memory cue did not match ($t = 6.98, P = 0.002$). The report of ipsilateral targets did not vary according to whether they matched the memory cue ($P > 0.05$). The impaired report of contralateral items on two-object trials was reduced when they matched the contents of working memory.

It could be argued that the patients might have been able to discriminate the color of the contralateral target regardless of whether it matched memory, and that any advantage for matching over nonmatching targets on the contralateral side could be due to patients then being biased to report the shape of the memory item, a form of sophisticated guessing from partial target information. This explanation seems quite unlikely, because there was no advantage for matching targets when just one object was displayed in the contralateral side, despite contralateral items having a lower probability of report than ipsilateral stimuli (see Fig. 2A). To test further against a sophisticated guessing account, we applied a quite conservative correction to

the data. In the condition in which the memory cue was absent in the following display, we scored as correct identifications trials those where just the color of the contralateral target was reported on two-item trials. This correction provides a measure of the maximum number of trials that would have been correctly reported in the condition when the memory item matched, if participants had seen the color of the contralateral item and guessed the shape of the memory cue. If sophisticated guessing of this type were responsible for the reduction in extinction, then we should find no difference between trials when the memory item was present and the rescored trials when the memory item was absent. Contrary to this proposal, the results were identical to before. There was extinction of contralateral targets [$F(1, 4) = 10.61, P = 0.031$], and this was modulated by the contents of working memory [$F(2, 8) = 8.56, P = 0.027$]. Contralateral targets were reported better when the memory item reappeared in the contra- compared with the ipsilateral field [$t(4) = 4.67, P = 0.01$], and compared with when it was absent [$t(4) = 3.6, P = 0.023$]. Thus, recovery from extinction in the working memory condition was greater than could be predicted on the basis of sophisticated guessing, where the color of the contralateral item was perceived and the shape of the memory cue guessed.

In addition to examining sophisticated guessing, we also evaluated the nature of the memory effects (Experiment 1a). One possibility is that the effects are based on a visual memory representation of the first stimulus. However, it could also be that the effects are due to a match between the properties of the memory item and the search items at a more abstract level, for example, based on common conceptual representations. To assess this possibility, we asked whether an abstract verbal description of the memory cue (i.e., green square) was sufficient to generate effects, or whether the memory cue needed to be visual. Two patients (BA and JB) were presented with verbal memory cues under identical conditions to those used with the visual memory stimuli (except that here, prime duration was 3

sec, to give patients enough time to read and memorize the verbal primes). Log-linear analyses assessed the number of correct to error trials as a function of the target's field (ipsi- vs. contralesional), and whether the memory and report displays matched. There was a significant effect of target field [$\chi^2(1) = 19.84, P = 0.00001$], showing extinction of contralesional targets. There was a trend for better performance when the memory cue matched rather than mismatched a target [$\chi^2(2) = 4.69, P = 0.09$; overall performance went from 74% on mismatching trials to 83.5% on matching trials], but this pattern did not vary as a function of target visual field [$\chi^2(2) < 1, P = 0.85$]. Verbal memory cues seemed to produce weaker effects than visual cues, and the effects were not specific to contralesional items. We suggest that abstract, semantic properties of the item held in memory need to be complemented by a visual memory representation of the first stimulus for this item to strongly modulate selection of the contralesional target.

In one additional control study (Experiment 1b), we evaluated whether the beneficial effects of memory matching found in Experiment 1 happened only for two-object trials, or whether the effects could be observed when just a single target is presented. In our initial study, performance on two-item trials was worse than on single-object trials; it could be that working memory effects depend on the level of performance, emerging only under more data-limited conditions, when target identification is more difficult. To test this hypothesis, four patients (BA, JB, RH, and TM) were reexamined in the one-object condition but using a shorter duration than before, to reduce the level of performance. Identification was marginally better for ipsi- than for contralesional targets [$F(1, 3) = 6.99, P = 0.077$]. However, there was only a trend for a beneficial effect of the memory cue [78% correct identification when the memory item and target matched vs. 66% correct when there was no match, $F(1, 3) = 6.01, P = 0.09$], and there was no interaction between matching to memory and the target's field [$F(1, 3) < 1, P = 0.42$]. This result suggests that the effects of working memory on parietal awareness are particularly tied to conditions where there is competition for selection between objects at different visual fields (on two-item trials) and not just to the overall level of performance.

In a second experiment (Experiment 2), the patients were merely exposed to the prime but were not required to hold it in memory. Here we found that identification was better with one than with two objects [$F(1, 4) = 14.53, P = 0.019$], and it was impaired in the contra- relative to the ipsilesional field [$F(1, 4) = 12.31, P = 0.039$]. Identification was also $\approx 3\%$ better with than without priming [$F(1, 4) = 20.29, P = 0.02$], but this small effect was additive across both visual fields (Fig. 2B). Further analyses in the two-object condition confirmed that identification of targets in each visual field was not modulated by the position of the primed object. Bottom-up priming was not sufficient to overcome competition for selection from the ipsilesional stimulus.

A third experiment (Experiment 3) was conducted to discard the possibility that the effects were not due to primes being committed to memory but to primes being processed to the level of identification. Note that identification need not occur when primes were viewed passively (Experiment 2). In Experiment 3, patients were required to verbalize the features of the prime before the onset of the target display. There was better performance with one than with two objects [$F(1, 4) = 9.17, P = 0.039$], along with extinction of contralesional targets on two-object trials [$F(1, 4) = 7.34, P = 0.054$]. Priming effects were absent ($P > 0.3$), even when primes were processed to the level of identification (Fig. 2C).

In Experiment 4, we retested three patients (BA, JB, and RH) in the memory condition but this time presenting the prime for 3 sec (the mean time taken to verbalize the prime in Experiment 3). Performance did not differ across experiments ($P > 0.26$).

False positives were minimal (mean 0.2%). Crucially, there was a significant interaction between memory matching and target field in the two-object condition [$F(2, 4) = 19.34, P = 0.046$], replicating the pattern found in Experiment 1 (Fig. 2D).

These data demonstrate that extinction is reduced when contralesional stimuli match the contents of working memory (Experiments 1 and 4). This same result does not occur with exactly the same displays when participants do not commit the cue to memory (Experiment 2), even if they identify the cue (Experiment 3). Extinction can be attributed to unbalanced spatial competition for stimuli to enter awareness, after a parietal lesion (13). Our data show that this competition can be rebalanced by top-down activation from items held in working memory, and items that achieve a match are given privileged access to awareness. The results fit with a reversed hierarchy framework in which awareness is achieved by reentrant activation of early visual areas (14). We suggest that reentrant activation from working memory can boost visual information that is impoverished by biased competition, making patients aware of contralesional items that they otherwise miss. Interestingly, the effects are particularly evident on two- rather than one-item trials, suggesting there is a greater effect on balancing competition for selection between the items than on improving the perception of the contralesional item *per se* (e.g., on one-item trials). It can be argued, given the evidence for a frontoparietal network controlling spatial attention and awareness (15–18), that prefrontal activation linked to working memory (19) could feed back to enhance activation in parietal cortex, presumably through spared parietal areas. Alternatively, the improvement in the patients' awareness could be achieved from prefrontal feedback through their intact ventral stream, which would activate features consistent with the memory item in striate and extrastriate cortex (6–8). Future work needs to separate these possibilities. In either case, though, the current study supports the importance of reentrant feedback from higher-order level areas for conscious visual experience.

Methods

Stimuli, Task, and Procedure. Displays were viewed from a distance of ≈ 60 cm. Each trial started with the presentation of a fixation point at the center of the screen. After the patients reported fixating on the central stimulus, a prime object was displayed for 1 (Experiments 1 and 2) or 3 sec (Experiments 3 and 4). The prime could be a circle ($1.8 \times 1.8^\circ$), a square ($1.5 \times 1.5^\circ$), a triangle ($2 \times 1.5^\circ$), or a diamond ($1.91 \times 1.91^\circ$). Two hundred milliseconds after the offset of the prime, either one or two objects were displayed along the horizontal plane with an eccentricity of 7.7° from the center of the screen. The colors used were red, blue, and yellow. The target objects in two-object trials were of different color. On 57.14% of the trials, one object matched the color and shape of the prime object, and on the remaining trials, the prime object and the target(s) differed in both dimensions. There was an equal likelihood of matching in the left and right visual fields. The prime was randomly selected across trials from 12 possible samples (four shape \times three color combinations), which meant that the probability of a cue being repeated in successive trials was $1/12 = 0.08$.

In Experiments 1 and 4, patients were asked to hold the prime in memory and were given instructions to form a mental image. In Experiment 2, the patients were merely exposed to the primes, and in Experiment 3, they simply had to verbalize the prime's features. Then they had to report the color and shape of the target object(s). The response was not force-choiced, to avoid guessing from the memory item when the patient was unsure or did not identify the color or shape of an object. The exposure duration for targets varied between 80 and 2,000 ms, depending on the severity of visual extinction for each patient. Durations were set to produce approximately the same level of perfor-

